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Seasonal and vertical distribution of a population of soil arthropods: Collembola

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With one Figure

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Contents

1. Introduction

Cyclic processes are a characteristic feature of animal populations, and they form an important aspect of population analysis. The processes can be of the short-term diurnal nature, which can be eliminated in data derived from the field by sampling at a standardised time of day, for example sun rise or sun set. Long-term cyclic processes are well-known in the mammals, but so far have not been demonstrated in the soil arthropods. The swarming of *Hypogastrura* (Christiansen 1964) suggests that long-term cycles may eventually be found within the Collembola. The mayor class of cylic processes are the seasonal ones, due largely to the breeding activity of the arthropods. Van der Drift (1951), Hale (1965, 1966a) and Healey (1967) have illustrated the seasonal trends in population size of Collembola in the field, and Christiansen (1964) and Hale (1967) have reviewed the literature concerning this cyclic process. Volz (1934), however, showed that there was a seasonal movement of the population, so that its location in the soil profile varied throughout the year. Two seasonal cycles, the numerical size of the population and the spatial distribution in the soil profile, have therefore been considered. Usher (1969) has discussed the size and distribution of aggregations of this population of Collembola.

The site from which the samples were taken is a Scots pine [*Pinus sylvestris* L. ssp. *scotica* (Schött) E. F. Warburg] forest on Cnoc Eòghainn in the Black Wood of Rannoch, Perthshire, Scotland (National Grid Reference NN 551546), at an elevation of 380 m. The sparse ground flora, mainly composed of three species, *Deschampsia flexuosa* (L.) Trin., wavy hair-grass, *Galium hercynicum* Weigel, heath bedstraw, and *Oxalis acetosella* L., wood-sorrel, is heavily grazed by sheep and deer. The quartzose felspathic schistose flags are overlain by glacial deposits, poor in nutrient status, giving rise to a humus-iron podsol. The litter horizon is 0.5—1 cm deep, the fermentation horizon 8—10 cm deep, and the humus horizon 15—18 cm deep. Samples have

been taken to a depth of 3 cm, and thus only from the litter and upper fermentation horizons. The physical and chemical aspects of the site are discussed more fully by USHER (1970).

Samples were collected on twelve occasions between October 1965 and October 1966. Two randomly located blocks of samples were collected, each block containing 48 contiguous samples arranged in a square four samples by four and three samples deep. Each individual sample was 4 cm square and 1 cm deep. The arthropods were extracted within three days of collection in a form of high gradient funnel apparatus. Details of the construction of the sampling device and of the extractor are given by USHER (1967). The arthropods were collected into picric acid, identified and counted. The soil samples were analysed for water content, pore space and for various chemical compounds.

2. Measurement of vertical distribution

If all of the arthropods in any particular core, which is divided into three samples each 1 cm thick, are considered to occur at the centre of the sample, then all the arthropods in the surface sample can be considered as occurring at a depth of 0.5 cm. Similarly, arthropods in the other two samples can be considered as occurring at depths of 1.5 cm and 2.5 cm respectively. If there are n_1 arthropods in the surface sample, n_2 in the centre and n_3 in the deeper sample, then the number of arthropods in the core, N, is:

$$N = n_1 + n_2 + n_3$$

and the weighted average, M, is

$$M = \frac{0.5\, n_1 + 1.5\, n_2 + 2.5\, n_3}{N}.$$

M is the 'centre of gravity' of the arthropods in the core, and is thus a statistic which reflects the depth of the arthropods in the soil. It can be used to compare the depth of populations sampled at different times of the year, or at different places. The statistic M will be referred to as 'mean depth'. It can vary between 0.5 (all of the arthropods in the surface of the core) and 2.5 (all of the arthropods at the bottom of the core). However, its use is limited by the fact that the value 1.5 can occur if all the arthropods are at the centre, or if half the arthropods are in the surface and half in the bottom layers, of by a number of other combinations. As the name 'mean depth' implies it gives an average value, but gives no information about the spread of the arthropods about this average. A further statistic, the 'depth deviation', can be calculated to show the spread of the arthropods about their 'mean depth'. This is analogous to the concept of the moment of inertia, and is calculated as:

$$S = \sqrt{\left\{\frac{n_1\,(0.5 - M)^2 + n_2\,(1.5 - M)^2 + n_3\,(2.5 - M)^2}{N}\right\}}$$

More generally, if there are k layers of samples with their centres at depths $d_1, d_2, \ldots, d_k$, then

$$N = \sum_{i=1}^{k} n_i$$

$$M = \frac{\sum_{i=1}^{k} d_i n_i}{N}$$

$$S = \sqrt{\left\{\frac{\sum_{i=1}^{k} n_i\,(d_i - M)^2}{N}\right\}} = \sqrt{\frac{1}{N}\left\{\sum_{i=1}^{k} n_i\, d_i^2 - \frac{\left(\sum_{i=1}^{k} n_i\, d_i\right)^2}{N}\right\}}$$

As an example of the calculations, on 20 February 1966 there were 6 *Isotomiella minor* in the samples from the surface layer, and 11 and 25 in the centre and lower layers respectively. This gives $N = 42$, $M = 1.952$ and $S = 0.730$.

3. Results and discussion

During the period of sampling a total of twenty four species of Collembola were found, though never more than eighteen species were recorded on any one sampling day. The total numbers of each species are shown in Table 1, throughout which the nomenclature follows GISIN (1960). Since the area of soil sampled during the year was 0.6144 m² this represents an average annual population density of 38,250 Collembola per m². Only seven of the species, *F. mirabilis*, *O. absoloni*, *T. callipygos*, *F. quadrioculata*, *A. binoculatus*, *I. minor* and *I. sensibilis* occurred in sufficient numbers throughout the year for detailed analyses of their distributions to be made. The species represented at Rannoch show some similarities with arctic and alpine faunas. MURPHY (1955) considered that *O. absoloni* is characteristic of alpine humus soils, whilst STACH (1947) considered that *A. binoculatus* is a winter species. *T. wahlgreni*, recorded only during the winter months, is a species that is abundant at altitudes over 1000 m on the mountains near to the site on Cnoc Eòghainn. This type of alpine fauna that occurs at Rannoch is one that has never been described in detail in the ecological literature.

Table 1. The species of Collembola collected during the sampling programme, October 1965 to October 1966. Nomenclature follows GISIN (1960).

Hypogastrura denticulata (BAGNALL)	1
Xenylla boerneri AXELSON	5
Willemia anophthalma BÖRNER	98
Friesea mirabilis (TULLBERG)	4305
Anurida granaria (NICOLET)	43
Neanura muscorum (TEMPLETON)	63
Onychiurus absoloni (BÖRNER)	7146
O. latus GISIN	200
Tullbergia callipygos BÖRNER	1995
Anurophorus laricis NICOLET	3
A. binoculatus (KSENEMAN)	593
Tetracanthella wahlgreni LINNANIEMI	42
Folsomia quadrioculata (TULLBERG)	3363
Isotomiella minor (SCHÄFFER)	797
Isotoma sensibilis (TULLBERG)	4309
I. viridis BOURLET	6
Isotomurus palustris (MÜLLER)	119
Entomobrya albocincta (TEMPLETON)	16
E. nivalis (L.)	5
Lepidocyrtus curvicollis BOURLET	81
Tomocerus minor (LUBBOCK)	12
Neelus minimus WILLEM	149
Sminthurides pumilis (KRAUSBAUER)	32
Dicyrtoma ornata (NICOLET)	114
Total number of Collembola	23497

Aspects of the climate of the Black Wood of Rannoch are shown in Fig. 1. The records are made about 5 km east-north-east of the sampling site, and at a slightly lower altitude. It will be noted that frosts are more or less absent only during the months June to September, though in some years frosts have occurred in all months. The warmest months are June and July, with an average temperature of 12.7 °C. The precipitation is spread, on average, more or less evenly throughout the year, but during the period of sampling July was an unusually dry month, and there were heavy snow falls during February.

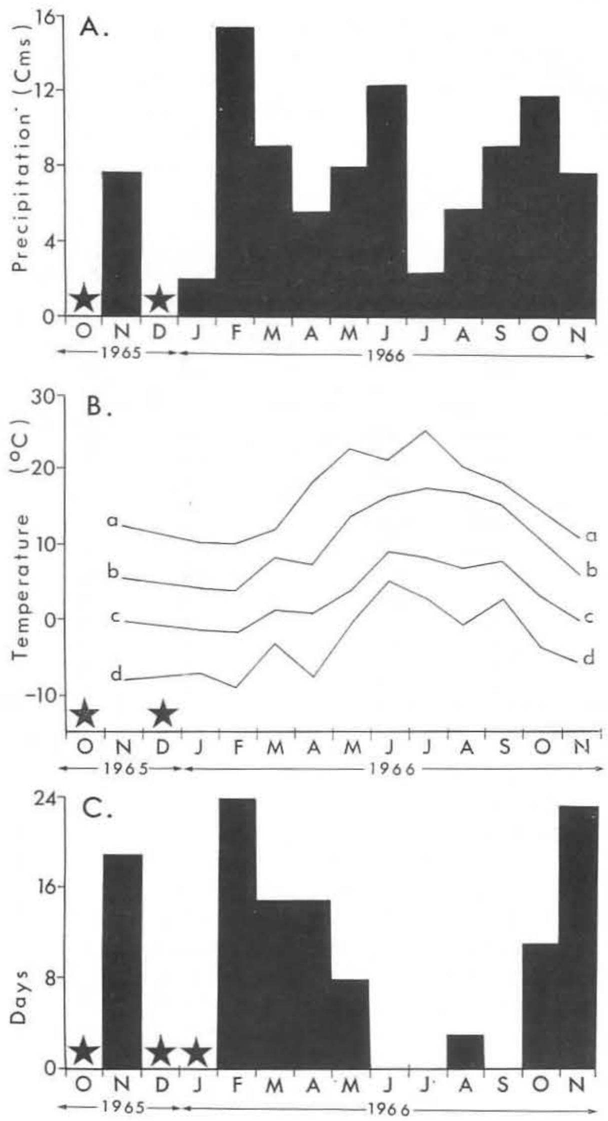

Figure 1. The climatic features of the sampling site at Rannoch. *A* shows the monthly totals for precipitation during the period of sampling October 1965 to October 1966. *B* shows the maximum (a), average maximum (b), average minimum (c) and minimum (d) temperatures. *C* shows the number of days in each month when the grass minimum temperature fell below 0 °C.

These climatic features of the site are presented since they are the most likely to affect the populations of soil arthropods.

3.1. *Friesea mirabilis*

This species has been recorded over a wide geographical range and from many habitat types (Da Gama 1964; Gisin 1960; Salmon 1964; Poole 1961; Hale 1966b). It was abundant at Rannoch, occurring with an average frequency of 7,010 per m². The data

in Table 2 show that there is only one annual peak in the population size, during the autumn, although the proportion of juveniles in the population increased in both the autumn and the spring. HALE (1966a) concludes that on moorland in Northern England there are annual peak population sizes of *F. mirabilis* in both the autumn and the spring. The Rannoch data suggests that this species is able to breed at all seasons, since on all sampling dates more than fifty percent of the population were juveniles, but that the main period of breeding is in the spring and autumn.

Table 2. The data for the adults and juveniles of *Friesea mirabilis* which show the number collected (N), the mean depth (M) and the depth deviation (D). The number of juveniles is expressed as a percentage of the total *F. mirabilis* population

Date of sampling	Juveniles			Adults			Percentage of juveniles in Total Population
	N	M	S	N	M	S	
31 x 65	229	1.86	0.72	126	1.83	0.69	65
21 xi 65	409	1.96	0.60	371	1.95	0.57	52
12 xii 65	106	1.93	0.63	85	1.80	0.74	55
16 i 66	55	1.30	0.77	34	1.62	0.80	62
20 ii 66	157	1.97	0.78	71	1.75	0.90	69
27 iii 66	58	1.14	0.71	29	1.53	0.89	67
1 v 66	197	1.51	0.76	43	1.64	0.88	82
5 vi 66	215	1.64	0.78	82	1.56	0.82	72
10 vii 66	151	1.76	0.85	138	1.76	0.74	52
14 viii 66	203	1.80	0.70	168	1.81	0.75	55
18 ix 66	380	1.84	0.66	350	1.76	0.69	52
23 x 66	446	1.88	0.71	202	1.96	0.62	69

The data for the mean depths (M) show that the vertical distribution of the juveniles is related to temperature. During the winter months the animals are deeper in the soil (M is about 1.9), and the depth deviation (S) is relatively small. In the summer the mean depth is less (M is about 1.7), but the value of S is greater indicating that the animals are more or less evenly spread through the three layers that were sampled. The adult *F. mirabilis* tend to show that they have the same vertical distribution as the juveniles, but the data for them are less clear. However, there is a correlation between the population size and the mean depth ($r = 0.679$ with 10 d. f.), showing that at times of maximum population size the animals are deeper in the soil profile. Similarly, the correlation between the mean depth and the depth deviation ($r = -0.835$ with 10 d. f.) shows that when the mean depth decreases the animals are more widely spread through the three layers sampled.

3.2. *Onychiurus absoloni*

GISIN (1960) records that this species has a wide European distribution, and that it is most frequent in acid soils. MURPHY (1955) considers it to be characteristic of alpine humus soils. It is, however, less common in Great Britain, since POOLE (1961, 1962, 1964) did not record it from his coniferous woodland sites, and HALE (1966a) found only one specimen amongst the twenty three thousand (approximately) that he recorded. The species was, however, the most abundant at Rannoch, occurring with an average annual frequency of 11,630 per m². There is only one peak population size in the year, and this is during the months August to November. The data in Table 3 show that the population size is small during the spring and summer, and that it starts to increase in July. The minimum population size was recorded during the months March to June.

The mean depth M appears to be related to both the population size and the temperature. During the period of the year February to July the value of the mean depth was

Table 3. The data for *Onychiurus absoloni* and *Tullbergia callipygos* which show the number collected (N), the mean depth (M) and the depth deviation (S)

Date of sampling	*O. absoloni*			*T. callipygos*		
	N	M	S	N	M	S
31 x 65	820	1.75	0.72	175	2.06	0.64
21 xi 65	1036	1.57	0.69	247	2.13	0.56
12 xii 65	148	1.65	0.77	42	1.81	0.69
16 i 66	358	1.30	0.86	36	1.48	0.80
20 ii 66	315	1.83	0.78	123	1.82	0.73
27 iii 66	203	1.68	0.81	38	1.70	0.80
1 v 66	223	1.69	0.74	57	1.54	0.75
5 vi 66	181	1.82	0.69	49	1.97	0.70
10 vii 66	440	1.70	0.77	124	1.87	0.76
14 viii 66	1243	1.55	0.81	599	1.75	0.75
18 ix 66	1094	1.52	0.76	328	1.72	0.78
23 x 66	1085	1.65	0.76	177	1.90	0.71

about 1.7 or greater, and during this period it can be seen in Fig. 1 that the average temperature was increasing. This is also the period of the year when the population size is small. During the months August to January the size of the population was either increasing or at a maximum, and the values for the mean depth mostly lie between 1.5 and 1.6. It will be seen from Table 3 that the values of the depth deviation are always large (0.69 and over), indicating that this species has no particular preference for any layer, but that it is well distributed throughout the upper horizons of the soil. However, the seasonal pattern indicates that there is some displacement of the population to the deeper horizons during the spring and summer.

3.3. *Tullbergia callipygos*

Although *T. callipygos* has a wide European distribution (Gisin 1960) it never seems to be abundant. Poole (1961) found that the ratio of *T. krausbaueri* to *T. callipygos* on his coniferous woodland site was approximately 10 : 1. However, at Rannoch, *T. krausbaueri* was absent from all the samples that were collected, and *T. callipygos* was the only species of the genus to be found. [Young specimens of *T. callipyois* seemed to be indistinguishable from the description of *T. macdougalli* given by Gisin (1960)].

The average annual population of *T. callipygos* at Rannoch was 3,250 per m². The data for the numbers of this species, given in Table 3, show that the peak population density was in August, and that a large population size was found from July to November. Hale (1966a) found that *T. krausbaueri* had a peak population size is summer and a second peak in early winter.

The mean depth appears to be related to neither the temperature nor the population size. However, it does very closely follow the rainfall, since at times of maximum precipitation (February, June and October) the mean depth is greater than at other times. The mean depth and the depth deviation are closely associated ($r = -0.837$ with 10 d. f.). Thus during the wettest periods of the year, *T. callipygos* is found deeper in the soil, and, since the depth deviation is smaller, it can be assumed that the animals are clustered into the lower horizons.

3.4. *Folsomia quadrioculata*

F. quadrioculata has been recorded over very wide geographical and edaphic ranges (Gisin 1960; Salmon 1964). The species was abundant at Rannoch with an average annual population density of 5,470 per m². Both Hale (1966a, b) and Poole (1961) have studied this species in Great Britain, but neither has separated the adults and juveniles

in their analyses. HALE (1966a) states that *Folsomia* spp. have two annual population maxima in Northern England, but at Rannoch only one maximum occurs (Table 4). There was a very large proportion of juveniles in the population in May, and this proportion decreases during the summer and early autumn. The data thus indicate that the juveniles form a considerable proportion of the population in late winter and spring, but that at all other times of the year the juveniles form between a quarter and a third of the population.

Table 4. The data for the adults and juveniles of *Folsomia quadrioculata* which show the number collected (N), the mean depth (M) and the depth deviation (S). The number of juveniles is expressed as a percentage of the total *F. quadrioculata* population

Date of sampling	Juveniles			Adults			Percentage of juveniles in Total Population
	N	M	S	N	M	S	
31 x 65	17	—	—	90	1.50	0.81	16
21 xi 65	48	1.50	0.76	121	1.41	0.70	28
12 xii 65	56	2.19	0.46	52	1.62	0.79	52
16 i 66	103	2.10	0.70	45	1.45	0.80	70
20 ii 66	72	2.35	0.46	173	1.52	0.80	31
27 iii 66	108	1.33	0.81	52	1.59	0.76	67
1 v 66	707	1.13	0.71	70	1.50	0.77	91
5 vi 66	124	1.48	0.73	162	1.50	0.78	43
10 vii 66	59	1.21	0.84	233	1.44	0.77	20
14 viii 66	147	1.27	0.78	419	1.57	0.72	26
18 ix 66	65	1.12	0.57	173	1.20	0.69	27
23 x 66	103	1.38	0.75	163	1.56	0.77	39

The mean depth of the juveniles closely reflects the temperature. During the winter months the juveniles are mostly in the lowest sample, with mean depths of more than 2.0. However, during the summer months the juveniles are at the surface, with mean depths less than 1.3. It will also be seen in Table 4 that the value of the depth deviation is minimal at both these periods, and it is greatest during the spring and autumn when the population is migrating.

Compared with the juveniles the adults have a very constant vertical distribution, since during most sampling periods the mean depth was close to 1.5 (Table 4). During all periods the depth deviation was large, indicating that the adult population was more or less evenly distributed throughout all layers sampled. USHER (1969) has commented on the fact that adult *F. quadrioculata* are the only Collembola at Rannoch to show a tendency to uniformity of their spatial distribution by not forming aggregations.

3.5. *Anurophorus binoculatus*

The data for this species are shown in Table 5, where it will be seen that the species was frequent during the early autumn and winter and infrequent during the spring and summer, indicating two peak population sizes in September/October and again in February. The average annual population size was 970 per m². The data for Rannoch support STACH's (1947) conclusions that *A. binoculatus* is a winter species.

The seasonal cycle of abundance of this species is closely correlated with temperature and frost. The advent of the early autumnal population increase coincides with the first time that the grass minimum temperature drops below 0 °C (Fig. 1 and Table 5), and reproduction during the winter months gives rise to the second peak population size recorded.

The mean depth of *A. binoculatus* varies considerably, but shows no correlation with either temperature or precipitation. Unfortunately the species was too scarce in a number

Table 5. The data for *Anurophorus binoculatus* and *Isotomiella minor* which show the number collected (N), the mean depth (M) and the depth deviation (S)

Date of sampling	*A. binoculatus*			*I. minor*		
	N	M	S	N	M	S
31 x 65	111	2.18	0.54	33	1.58	0.67
21 xi 65	20	—	—	7	—	—
12 xii 65	12	—	—	14	—	—
16 i 66	41	1.41	0.78	92	1.43	0.81
20 ii 66	118	1.49	0.83	56	1.82	0.76
27 iii 66	9	—	—	78	1.69	0.77
1 v 66	29	1.50	0.74	82	1.80	0.73
5 vi 66	5	—	—	90	1.59	0.64
10 vii 66	13	—	—	68	1.57	0.72
14 viii 66	24	1.88	0.69	133	1.86	0.72
18 ix 66	144	1.58	0.68	87	1.36	0.53
23 x 66	67	1.53	0.68	57	1.50	0.88

of blocks of samples for an estimate of the mean depth and the depth deviation to be calculated.

3.6. *Isotomiella minor*

Van der Drift (1951) found that this species had a seasonal fluctuation with an August maximum and a January minimum population size. The study at Rannoch has similarly shown that there is an August maximum population size (Table 5), and that the minimum occurs in November and December. The species was frequent at Rannoch with an average annual population density of 1,300 per m^2.

The seasonal cycle of population size seems to be only distantly related to the temperature cycle, since the population maximum occurs a month after the temperature maximum, and the population minimum two months before the temperature minimum. However, the average temperature drops very rapidly from July to Nevember, and then only drops slightly from November till January or February (Fig. 1). It thus seems that the size of the population is influenced by the increasing temperature during the spring, and by the rapid fall in temperature during the autumn. The mean depth of the animals is unrelated to the climate. Table 5 shows that the depth was greatest in February, May and August, which are months with contrasted temperature and precipitation. The data show that the mean depth was least in January and September, also months with contrasted climatic features. There is thus no evidence that the climate influences the vertical distribution of *I. minor*.

3.7. *Isotoma sensibilis*

The development of this species has been studied by Hale (1965) who found that egg laying in Northern England takes place in April, and that the development period of the eggs is about three weeks. The data for Rannoch (Table 6) support Hale's conclusion, since there were large numbers of juveniles in the samples taken in May and June, and at these times the juveniles formed 70 to 73 % of the *I. sensibilis* population. However, there was a relatively high proportion of juveniles in the population at all times of the year (except October 1965), indicating that there is breeding throughout the year but that it is most intense during April and May. Laboratory studies, Usher (1964), indicated that the juvenile stage is of about 26—30 days duration at 19 °C. The season of breeding is at a time of rising mean temperature, and breeding commenced when the mean daily temperature reached about 5 °C.

Table 6. The data for the juvenile and adult forms of *Isotoma sensibilis* which show the number collected (N), the mean depth (M) and the depth deviation (S). The adults collected on 31 October and 21 November 1965 were not sorted into the two colour types. The number of juveniles, which could not be sorted into colour types, is expressed as a percentage of the total *I. sensibilis* population

Date of sampling	Juveniles			Pale Adults			Dark Adults			Percentage of Juveniles in Total Population
	N	M	S	N	M	S	N	M	S	
31 x 65	57	1.13	0.66	182	1.00	0.69	*	*	*	24
21 xi 65	236	0.81	0.49	291	1.05	0.60	*	*	*	45
12 xii 65	150	0.90	0.57	58	0.80	0.56	39	0.99	0.76	61
16 i 66	275	0.99	0.72	102	1.00	0,70	54	1.25	0.82	64
20 ii 66	272	1.90	0.76	47	1.01	0.71	64	1.27	0.72	71
27 iii 66	147	1.05	0.62	88	0.77	0.53	38	0.82	0.64	54
1 v 66	395	1.07	0.68	134	1.01	0.74	35	1.07	0.73	70
5 vi 66	515	1.08	0.64	118	0.94	0.62	74	1.03	0.60	73
10 vii 66	158	0.79	0.56	50	0.78	0.53	24	1.00	0.71	68
14 viii 66	165	1.03	0.67	81	1.06	0.76	30	0.95	0.63	60
18 ix 66	96	0.82	0.63	83	0.70	0.50	51	0.70	0.49	42
23 x 66	97	1.04	0.67	42	1.05	0.73	61	0.85	0.62	59

I. sensibilis is abundant at Rannoch, with an average annual population density of 7,010 per m². The adults show two distinct colour varieties — dark blackish-violet (dark adults) and greenish-brown (pale adults). Hale (1966b) records these two colour types from his moorland sites, and suggests that the pale forms are associated with mineral soils and some areas of *Sphagnum* and *Polytrichum* mosses whilst the dark form is characteristic of peat soils. Usher (1969) shows that there are differences in the spatial distribution of these two colour types, and that the juveniles and pale adults have a similar form of distribution. The juveniles were too poorly pigmented to be assigned to either of the colour types.

The seasonal fluctuations of the adult population reflect those of the juveniles, with large population sizes following maxima in the juvenile population size. However, the numbers of pale and dark forms are not correlated ($r = 0.050$ with 8 d. f.), indicating the temporal separation of the peak population sizes of these two colour types. Table 6 shows that on all sampling dates the proportion of dark adults was between 25 and 40% of the adult population, except in February and October when the proportions were 58 and 59% respectively. These two months correspond to the maxima in the population size of the dark adult form, and the minima in the population size of the pale form. It can be noted from Fig. 1 that the population maxima of the dark adult form correspond with seasons of peak rainfall, but it seems unlikely that this is a true relationship.

The data for the mean depth of *I. sensibilis* (Table 6) indicate that this is a species of the soil surface. The mean depths usually lie between 1.0 ± 0.1 cm, except in February 1966. This month was the coldest, and had more frost than any other, and it seems likely that there was a vertical movement of the population under these extreme conditions. The mean depth of the juveniles was 1.9 cm, though the depth deviation of 0.76 indicates that the juveniles were widely distributed throughout the layers. The data indicates that vertical migration is a response only to extreme conditions of cold near the soil surface, and that the drying of the litter and fermentation horizons in the summer had little effect on the vertical distribution of *I. sensibilis*.

3.8. Other species

Burges (1963) states that the oil on the bearing of an engine is vital although its "biomass" compared with that of the engine is insignificant. This is important to remem-

ber when discussing soil arthropod communities, since in most studies only about a quarter of the species are frequent enough for statistical analysis of their data. In the present study only seven of the twenty four species listed in Table 1 have been frequent enough for detailed analysis of the seasonal and vertical distributions. However, a further six species were collected on at least eleven of the twelve dates when samples were taken. These species are *Willemia anophthalma*, *Neanura muscorum*, *Onychiurus latus*, *Isotomurus palustris*, *Neelus minimus* and *Dicyrtoma ornata*.

W. anophthalma occurred infrequently at all times of the year, with an average population of 200—300 per m². However, samples taken in January and again in June and July exceeded this with a population density of 620—740 per m². It therefore seems that there are two annual maxima, one occurring in the winter and the other in the summer. *N. muscorum* showed a less obvious pattern of seasonal fluctuation. It was not recorded in December 1965, but on the four sampling dates between January and May 1966 about two thirds (43 out of 63) of the total number were collected. This shows that *N. muscorum* is a winter species, being more abundant during the winter months. Its average annual population density at Rannoch was about 200 per m².

The population density of *O. latus* fluctuated between 0 and 3,200 per m², with the maxima occurring in January, and during September and October. It therefore seems that this species has two maximum populations in the year, in winter and in the autumn. HEALEY (1967) working on the closely related species *O. procampatus* showed a very similar seasonal cycle with maximum population sizes in the autumn and winter.

I. palustris similarly shows a fluctuating population density, varying between 40 and 1560 per m². The two maxima in the numbers occur in March and again in September and October, with minima during November and December and during June and July. *N. minimus* had an almost stable population density of 200 per m² throughout the year, except in September 1966 when the density rose to 3,800 per m². The reasons for this one set of samples yielding such a high density are not clear, and since samples collected in August and October 1966 had the average population density it seems unlikely that Rannoch data shows any seasonal cycle. *D. ornata*, however, shows a clear annual cycle. Peak population sizes occur during the late winter and early spring months, since 84 of the 114 *D. ornata* collected were in samples taken in January, February, March and May 1966. This species also shows a distinct vertical migration at this time of the year. Normally it is found on the surface on the soil, but during the cold winter months it is at a mean depth of 1.5 to 1.7 cm. During January and February there were a large number of juveniles amongst the population of *D. ornata*.

A further five species, *Anurida granaria*, *Entomobrya albocincta*, *Lepidocyrtus curvicollis*, *Tomocerus minor* and *Sminthurides pumilis*, were collected on between five and nine of the twelve occasions when samples were taken. Three of these species show distinct summer and autumn maximum population sizes. The maxima for *A. granaria* and *E. albocincta* are during July to September, and for *L. curvicollis* the maximum is during June to August. This latter species was not collected during November, December or January, but was found during all other months of the year. HALE (1965) states that the eggs of this species are laid during October and November, and that eggs hatch by April. *S. pumilis* had a maximum population density during the late autumn and winter (October to February inclusive), and it was absent from all samples collected during the period May to August inclusive. *T. minor*, however, has a late winter maximum population size (February to May), and was absent from all samples collected during the period August to November inclusive. SHARMA (1967) shows that *T. vulgaris* overwinters in the adult stage in Canada, and KNIGHT (1963) shows that the maximum population size of *T. flavescens* occurs in the spring, with juveniles being found in the population from December to April. It therefore seems likely that *T. minor* at Rannoch

has the winter population maximum, with eggs being laid in March and April [Sharma (1967) quotes these months for there species of *Tomocerus* other than *T. minor*], and the eggs hatching during December and January.

Finally, there are six species that occurred on three or less of the dates when samples were collected. *Xenylla boeneri* was only collected in August, October and November; *Anurophorus laricis* in May and October; *Tetracanthella wahlgreni* in October and November; *Isotoma viridis* in May and June; *Hypogastrura denticulata* in June; and *Entomobrya nivalis* in August. The only tentative conclusions about this group of species are that *X. boerneri* and *T. wahlgreni* have peak population sizes in the autumn, whilst *I. viridis* has its population maximum in the summer.

4. Conclusions

The majority of species of Collembola at Rannoch have only one peak population size each year, allowing a classification of the species into groups according to the time of year when they were most abundant. The winter species, including *S. pumilis*, *N. muscorum*, *D. ornata* and *T. minor*, have peak population densities in the months between December and March. *S. pumilis* populations reached their maximum size during December, and declined until the species was absent from samples collected in March. However, the populations of the other three species in this group increased in size during December and January, reached their maximum in March, and were either absent or very scarce by June.

A second group of species are the spring Collembola, most of which show breeding activity at this time of the year. The peak population density of *F. quadrioculata* juveniles was reached in May, whilst the peak adult population was achieved in August. Similarly, peak population densities of *I. sensibilis* (juveniles and pale adults) were observed in May and June, which was also the only time of the year when *I. viridis* was collected.

The summer species include *L. curvicollis*, which was most abundant during June, July and August, and *I. minor* which has an August maximum population density. Both *A. granaria* and *E. albocincta* were most abundant during the late summer months, July to September.

Three of the five most abundant species have peak population densities during the autumn. These species, *T. callipygos*, *O. absoloni* and *F. mirabilis*, account for 57 % of the total number of Collembola collected. All three species have maximum population densities in September and October. Later in the autumn, in October and November, *X. boerneri* and *T. wahlgreni* reach their maximum populations sizes.

Five species do, however, show two peaks in their population size distribution. Four of these, *O. latus*, *A. binoculatus*, *I. palustris* and the dark adult form of *I. sensibilis*, have peak population densities in the winter months (January, February or March) and in the autumn (September and October). Excepting *I. sensibilis*, the number of animals in the autumnal populations was greater than that in the winter population. *W. anophthalma* showed a similar distribution, but the population maxima occurred in January and in June and July, winter and summer. None of the species showing two peak population densities in the year was abundant.

It is clear that the majority of the species of Collembola at Rannoch, and certainly all of the most abundant species, show only one annual maximum in their population densities. This contrasts with Hale's (1966a) study of moorland Collembola in Northern England, where many species were shown to have more than one peak population size during the year. The climatic conditions at Rannoch are severe, and an arctic alpine influence is noted in the fauna by such species as *O. absoloni*, *A. binoculatus* and *T. wahl-*

greni. Under these cold and wet climatic conditions the majority of the species forming the Collembolan population have only one population maximum during the year.

The climate affects the vertical distribution of the Collembola as well as their actual population size. HALE (1966a) asks whether this is due to the animals moving in response to the conditions of their environment, or whether there is a differential mortality in the different strata of the soil profile. The studies quoted in MURPHY (1962) and by MACFADYEN (1962) show that soil arthropods will move in relation to changing environmental conditions. The rapid changes in the vertical distribution of *I. sensibilis* and *D. ornata* that have been observed at Rannoch are not associated with any decrease in the population size, but rather with a large increase in the layer in which they are newly found. It therefore seems that vertical migration takes place, and that differential mortality can only account for a small proportion of the observed changes in the vertical distribution.

The only species at Rannoch frequent enough for the analysis of their vertical distribution were *F. mirabilis*, *O. absoloni*, *T. callipygos*, *F. quadrioculata*, *A. binoculatus*, *I. minor*, *I. sensibilis* and *D. ornata*. Neither *A. binoculatus* nor *I. minor* showed any relationship between their vertical distribution and the climate. The precipitation at Rannoch was related to the vertical distribution of *T. callipygos*, since at times of greatest precipitation the species was deepest in the soil profile.

Temperature is the most important feature causing vertical migration. *I. sensibilis* is a species generally confined to the surface of the soil profile, living in the litter horizon and not penetrating far into the fermentation horizon. However, during the coldest month of the year there was a migration of this species into the fermentation horizon, resulting in an average displacement of about 1 cm per individual. Similarly, *D. ornata* was usually found on the surface of the pine needles composing the litter horizon, but during the coldest months of the year there was a displacement of up to 1 cm per individual into the fermentation horizon.

F. mirabilis and *F. quadrioculata* showed a seasonal migration, since their mean depths were greatest during the coldest months of the year. During the time of milder conditions from April to November, the adults and juveniles of *F. mirabilis* were well distributed throughout the three layers sampled. However, the juveniles of *F. quadrioculata* came towards the surface of the soil profile during the warm summer months. *F. quadrioculata* juveniles show a close relationship between temperature, mean depth and the depth deviation. The depth deviation is minimised both during the warmest and the coldest months of the year. The adults of *F. quadrioculata*, however, showed no vertical migration. *O. absoloni* also moved in relation to the season of the year. It appears to be deeper in the soil during the period from February to July, whilst the mean temperature of the site was increasing, and to be well distributed throughout all of the layers sampled whilst the mean temperature is falling and at a minimum. The reason for this is unknown.

Thus, it appears that the climate of the site at Rannoch has three main influences on the population of soil Collembola. Firstly, the faunistic influence determines which species are present. This does not only determine which species are abundant, but some of the infrequent species show the relation between the Rannoch fauna and the arctic alpine faunas. Secondly, the breeding activity and thus the numerical abundance of individual species is dependent upon the climate. The majority of species at Rannoch have only the one maximum population size per year, contrasting with environments that are further south and warmer. Thirdly, climate determines the vertical distribution of a number of species in the soil profile. These vertical migrations have been shown for a few of the species that where abundant at Rannoch, but it seems likely that more of the species would demonstrate vertical movements during the year if there had been sufficient data for statistical analysis.

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